

DEMOGRAPHY OF *ASTRAGALUS SCAPHOIDES* AND EFFECTS OF HERBIVORY ON POPULATION GROWTH

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ABSTRACT.—Losses in fecundity due to predispersal herbivory can be large; however, the effects of this loss on long-term population viability have rarely been investigated. I conducted a demographic study of *Astragalus scaphoides* (Fabaceae), a long-lived perennial endemic to east central Idaho and adjacent Montana, by following mapped individuals at two sites from 1986 to 1993. *Astragalus scaphoides* suffers losses of predispersal fecundity averaging nearly 50% from insect seed predation and inflorescence predation by insects and livestock. Cattle reduced fecundity by 0–85%. Nonetheless, estimates from matrix projection models indicate that both sample populations had positive growth in most years. Elasticity analyses revealed that population growth occurred in spite of relatively small contributions by recruitment compared to growth and survival of nonreproductive plants. Results suggest that populations of this long-lived perennial depend little on reproduction and recruitment for growth and can persist in association with seasonal-rotation livestock grazing.

Key words: demography, herbivory, livestock grazing, predation, matrix projection models, elasticity analysis, *Astragalus*, rare plant.

The importance of herbivory in determining plant population dynamics and composition of vegetation has long been debated (Ehrlich and Birch 1967, Slobodkin et al. 1967, Belsky 1986). A great deal of evidence suggests a negative impact of herbivory on the host plant (Harper 1977, Crawley 1983, Dirzo 1984); however, researchers have recently presented evidence for positive interactions (McNaughton 1986, Paige and Whitham 1987).

A plant's life history plays an important role in determining the effects of herbivory. Loss of reproductive output from seed predators can be disastrous for an annual or biennial but may have little effect on a long-lived perennial. Furthermore, effects of herbivory will depend on the age or stage (e.g., seeds, adults) at which it occurs (Dirzo 1984). Most studies have focused on the effects of herbivores on particular components of fitness over relatively short time spans. This is unfortunate because it is the long-term effect on population growth that determines the importance of herbivory to population viability. Few studies have integrated the effects of herbivory on population dynamics and growth (Harper 1977; but see Louda 1982, 1983).

Predation, particularly by exotic species, has often been cited as a threat to endangered plant populations (Greig-Smith and Sagar 1981, Parsons and Browne 1982, Willoughby 1987, Norton 1991, Pavlik et al. 1993). Negative impacts of herbivores were shown, but a causal link to declining population size has rarely been demonstrated.

Astragalus scaphoides (Jones) Rydb. is endemic to a small area of east central Idaho and adjacent Montana (Barneby 1964). It was formerly a candidate for listing as a threatened or endangered species by the U.S. Fish and Wildlife Service (Category 3C; USD1–FWS 1993) and is currently listed as sensitive in Idaho (Moseley and Groves 1990) and Montana (Lesica and Shelly 1991). Most populations of *A. scaphoides* occur on public lands subject to livestock grazing. High levels of inflorescence and seed predation have been observed in some populations (Lesica and Elliott 1987a). Here I report the results of an eight-year demographic study of *A. scaphoides* at two sites. The purpose of the study is to document levels of herbivory and to assess its importance to population growth using stage-based transition matrix models and elasticity analysis (de Kroon et al. 1986, Caswell 1989).

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METHODS

Species Studied

Astragalus scaphoides is a caulescent perennial with a taproot surmounted by a branched caudex. Reproductive individuals are 20–50 cm high with a cluster of pinnately compound basal leaves and 3–10 leaves at intervals along the erect stem. The inflorescence is composed of 1–4 racemes arising from the axils of the upper leaves. Each raceme is composed of a naked peduncle, 5–15 cm long, surmounted by a tight cluster of 10–30 flowers that expands in fruit. Nonreproductive individuals generally have 1–4 basal leaves and may have a sterile stem less than 15 cm tall with 1–5 leaves. The branching caudices of reproductive plants may bear up to four stems and more than a dozen racemes (Barneby 1964, Lesica unpublished data).

Astragalus scaphoides generally flowers during the first three weeks of June. The most conspicuous form of herbivory of these plants is the removal of inflorescences during flowering. Inflorescence predation has two principal sources: insects and livestock. Ants (subfamily Formicinae) and moth larvae (*Melacosoma* spp., family Lasiocampidae) were observed removing inflorescences at a site near Haynes Creek in Idaho. Peduncles below the flowers were girdled, and withered inflorescences were often still present near the base of the plant. Inflorescence predation by livestock also occurred but differed from insect predation in that peduncles were all removed at the same height, and severed inflorescences were not found below the plants. In either case the cluster of basal leaves was usually left intact. It was possible to assign primary responsibility for inflorescence herbivory at a site in a particular year to either insects or ungulates based on the appearance of damaged plants and the presence or absence of droppings, hoof prints, or trampled vegetation. However, it was not possible to unambiguously assign each case of herbivory to one or the other source. Inflorescence predation by insects was observed at both study sites in all years that inflorescences were produced, but ungulate predation was common only at Sheep Corral Gulch.

Predispersal seed predation occurred at both sites in most years. Larvae were collected from developing legumes in 1986 and identi-

fied as weevils, small beetles in the family Curculionidae. Weevil larvae feed on maturing seeds and leave the developing or mature legume by creating a small hole in the outer wall. Seed predation by weevil larvae was inferred from the presence of fecula and/or an exit hole in the legume.

Study Sites

The Sheep Corral Gulch population occurs in southern Beaverhead County, MT, on a gentle south-facing slope at 1920 m (T8S R12W S16). Mean July and January temperatures at Dillon, 32 km NW and 275 m lower, are 19.0° and –6.6° C, respectively. Mean annual precipitation is 241 mm. Vegetation is dominated by *Artemisia tridentata* and *Agropyron spicatum*. *Aster scopulorum* and *Phlox hoodii* are common forbs. Livestock were managed on a rest-rotation system by which grazing occurred in different seasons in most consecutive years. Evidence of heavy spring grazing by livestock was observed in 1989, 1990, and 1993.

The Haynes Creek population is in central Lemhi County, ID, approximately 48 km W of Sheep Corral Gulch. It occurs on a moderate southeast-facing slope at 1555 m (T19N R23E S2). Mean July and January temperatures at Salmon, 24 km NW and 365 m lower, are 16.2° and –6.7° C, respectively. Mean annual precipitation is 252 mm. Vegetation is dominated by *Artemisia tridentata*, *Agropyron spicatum*, and *Bromus tectorum*. This site was not grazed by livestock before early July during the course of the study.

Field Methods

Two permanent monitoring transects were established at each of the study sites in early July 1986 following methods outlined in Lesica (1987). Transects were located subjectively to represent the populations and were read in early July because fruits were mature or nearly so, but seed dispersal had not yet begun. At each site the transects were parallel to each other and the slope. Each transect consisted of 50 adjacent 1-m² mapping quadrats placed along the transect line. The position of each *A. scaphoides* plant encountered in the quadrats was mapped and classified for three traits: (1) size, (2) inflorescence production, and (3) fecundity using the following classification:

- (1) Size classes:
 - D Dormant (no aboveground parts observed)
 - S Small nonreproductives (1-3 leaves)
 - L Large nonreproductives (≥ 4 leaves)
 - R Reproductive
- (2) Inflorescence production:
 - A Inflorescence produced no fruit
 - P Inflorescence was removed due to predation
 - I Inflorescence produced at least one mature fruit
- (3) Fecundity: total number of mature fruits

When stems were removed below the point of inflorescence articulation, I made a conservative estimate of the number of inflorescences removed based on the size of the remaining plant. Evidence of livestock and native ungulates (e.g., droppings, hoof prints, trampled vegetation) was noted along each transect and for the site as a whole.

I found that some plants would go undetected for one to several years but reappear in subsequent years (Lesica and Steele 1994). These "dormant" plants may have produced small leaves that had senesced and disappeared by early July; however, my observations in May and June suggest that most of them produced no vegetation on the years in question. The presence of dormant plants can be inferred by comparing transect maps from the full sequence of years. The proportion of dormant plants ranged from 1% to 23%, with a mean of 10% in 1987–1991. Plants have "disappeared" for as many as five years before reappearing. However, in 1986–1992 at the two sites, 71% of dormant plants reappeared after one year, and 88% reappeared after two years (Lesica and Steele 1994). As a result, ca 10% of the plants were undetected in the first and last years of the study, and ca 3% were undetected in the second and second from last years. Thus, I have chosen to eliminate the first and last years (1986, 1993) of the study from demographic analysis, recognizing that a small (ca 3%) error still remains in mortality and recruitment estimates in 1987 and 1992.

On years when fruit production was adequate, I collected 50 randomly selected mature fruits from at least 25 plants. I opened

the pods, counted intact seeds, and recorded evidence of insect predation.

Data Analysis

Stage-structured transition matrix projection models summarize the way in which survival, growth, and reproduction at various life-history stages interact to determine population growth (van Groenendaal et al. 1988, Caswell 1989). Matrix projections assume fixed transition probabilities between stages in a population through time (Lefkovitch 1965, Menges 1990). They also assume density-independent population growth and thus do not give an accurate projection of long-term population future. Nonetheless, they can be used to summarize short-term population dynamics (Caswell 1989). One-year transition probabilities were estimated as the number of plants in life-stage class i moving into class j over the course of one year divided by the number of plants in stage i at the beginning of the year. This method assumes that an individual's transition depends only on its life-stage class at the beginning of the period and is independent of its transition the previous year. The equilibrium growth rate (λ) is the dominant eigenvalue of the transition matrix (Lefkovitch 1965, Caswell 1989). $\lambda > 1.0$ indicates population increase, while $\lambda < 1.0$ indicates decrease. λ integrates the effects of survival, growth, and fecundity of the different life-history stages into a single parameter. There are two ways in which a reproductive plant can undergo a transition: (1) the plant itself moves into a different class or stays the same and (2) the plant produces progeny in one or more classes. These two probabilities (Recruit, Repro) are presented separately in the matrices but must be added together to solve for λ . Details on the construction and use of matrix population models can be found in Caswell (1989) and Menges (1990). λ was calculated using RAMAS/stage (Ferson 1991).

Elasticity measures the relative change in the value of λ in response to changes in the value of a transition matrix element. Elasticity matrices allow comparison of the relative contributions of various life-history transitions to population growth and fitness (de Kroon et al. 1986). Elasticities sum to unity, and regions of the matrix may be summed to compare the importance of growth and survival to recruitment

(Caswell 1989). Elasticities for nonreproductive plants are sums from the small (S) and large (L) classes. Elasticities were calculated using RAMAS/stage (Ferson 1991).

When the majority of seeds pass directly from production to germination in less than one year, seeds should not appear as a separate stage in matrix models (Caswell 1989, Silvertown et al. 1993). Seeds of *Astragalus scaphoides* germinate readily without stratification (Lesica and Elliott 1987b), suggesting that most seeds germinate the same year they are produced. Nonetheless, *A. scaphoides* may form a seed bank. Not including a seed bank in the matrix model may affect the value of λ (Kalisz and McPeck 1992), especially when it is <1.0 . However, it will have little effect on analyses based on elasticities (Silvertown et al. 1993). I calculated separate elasticities for reproductive transitions and recruitment by dividing the reproductive + recruitment elasticities proportionately between the two components.

Losses to predation were estimated from the number of inflorescences lost using the calculated means for seeds/fruit and fruits/inflorescence. Cumulative fecundity losses were calculated by multiplying the proportions of inflorescences and seeds remaining after predation and subtracting from one.

RESULTS

Population Growth

The number of *Astragalus scaphoides* plants in the transects at both sites increased by about one-third between 1986 and 1993 (Fig. 1). Equilibrium population growth rate (λ) was ≥ 1.0 at both sites over the course of the study and was >2.5 at Sheep Corral Gulch in 1988–89 and 1990–91. At no time during the study was $\lambda < 0.8$ at either site (Table 1).

Survivorship

Between 40% and 50% of the *Astragalus scaphoides* plants observed at the start of the study in 1986 were still alive in 1993 (Fig. 2). Approximately 50% of the 1989 cohort (the first large cohort recruited during the study) survived for more than 3–4 years. Taken together these results indicate that *A. scaphoides* is a long-lived perennial, with ca 50% mortality occurring in the first 3–4 years, but a large proportion of plants living to be ≥ 10 years.

Predation

Inflorescence predation attributable to ungulates was virtually absent from the Haynes Creek population. Droppings and hoof prints of cattle were the only signs of ungulates at Sheep Corral Gulch. Droppings occurred in 3–9% of the mapping quadrats during the study. Inflorescence predation by insects occurred at both sites in all years.

A significant number of inflorescences were produced in six of eight years at Haynes Creek, and inflorescence predation accounted for fecundity losses of 14–50% over the course of the study (Fig. 3). Most of this herbivory was attributable to insect damage. At Sheep Corral Gulch reproductive plants were common in only four of eight years. Inflorescence predation resulted in fecundity losses of 19–90%, and the proportion of inflorescences lost to predation was highest in 1989, 1990, and 1993, years in which predation was due mainly to livestock (Fig. 3).

Seed predation occurred at both sites in nearly every year in which significant fruiting occurred (Fig. 3). Overall, loss of seeds to weevil predation ranged from 0 to 33% with a mean of 18%. Insect seed predation was generally higher at Sheep Corral Gulch than at Haynes Creek (Fig. 3).

Losses of fecundity due to the combined effects of inflorescence and seed predation were 19–90% in 1986–1993, with means of

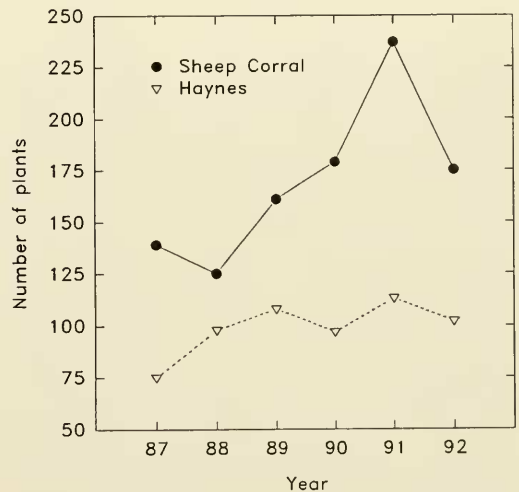


Fig. 1. Density of *Astragalus scaphoides* plants in the two sample populations, 1987–1992.

TABLE 1. Stage-based transition matrices for *Astragalus scaphoides* at two sites in 1987–1992. Four stages are recognized: dormant (D), small nonreproductive (S), large nonreproductive (L), and reproductive (R). The reproductive and recruitment (Rc) columns must be added together before solving for λ , the dominant eigenvalue (see Methods).

----- Sheep Corral Gulch -----

1987-88						1990-91					
To	From					To	From				
	D	S	L	R	Rc		D	S	L	R	Rc
D	.67	.18	.20	0	+ 0	D	.14	.06	0	0	+ 0
S	.11	.55	.24	0	+ 0	S	.21	.23	.06	0	+ 9.86
L	.22	.06	.36	0	+ 0	L	.50	.42	.26	.29	+ 2.42
R	0	0	.03	1.0	+ 0	R	.14	.12	.57	1.0	+ .14
$\lambda = 1.18$						$\lambda = 2.69$					
1988-89						1991-92					
To	From					To	From				
	D	S	L	R	Rc		D	S	L	R	Rc
D	.23	.04	.02	0	+ 0	D	.70	.24	.21	.25	+ 0
S	.17	.27	.05	0	+ 4.0	S	.30	.27	.37	.33	+ .20
L	.43	.53	.45	0	+ 7.0	L	0	0	.14	.22	+ 0
R	.17	.08	.43	1.00	+ .25	R	0	0	0	0	+ 0
$\lambda = 2.51$						$\lambda = 0.83$					
1989-90											
To	From										
	D	S	L	R	Rc						
D	.80	.17	.14	.06	+ 0						
S	.10	.73	.37	.22	+ .91						
L	.10	.02	.35	.56	+ .03						
R	0	.02	.01	.16	+ 0						
$\lambda = 0.97$											

----- Haynes Creek -----

1987-88						1990-91					
To	From					To	From				
	D	S	L	R	Rc		D	S	L	R	Rc
D	.50	.03	.04	0	+ 0	D	.21	.03	0	0	+ 0
S	.40	.45	.04	0	+ 5	S	.21	.34	.03	0	+ .95
L	0	.24	.37	0	+ .16	L	.50	.31	.21	.18	+ .27
R	.10	.06	.52	.60	+ .20	R	.07	.19	.66	.64	+ 0
$\lambda = 1.88$						$\lambda = 1.31$					
1988-89						1991-92					
To	From					To	From				
	D	S	L	R	Rc		D	S	L	R	Rc
D	.57	.13	.04	0	+ 0	D	.75	.03	.06	.05	+ 0
S	.14	.42	.24	.05	+ 1.10	S	0	.44	.30	.15	+ .30
L	.14	.16	.28	.14	+ .14	L	.25	.08	.36	.53	+ .03
R	.14	.04	.32	.67	+ .05	R	0	0	.11	.20	+ 0
$\lambda = 1.13$						$\lambda = 0.83$					
1989-90											
To	From										
	D	S	L	R	Rc						
D	.64	.12	.05	0	+ 0						
S	.27	.38	.14	.04	+ .23						
L	0	.20	.48	.27	+ .04						
R	.09	0	.33	.58	+ 0						
$\lambda = 0.97$											

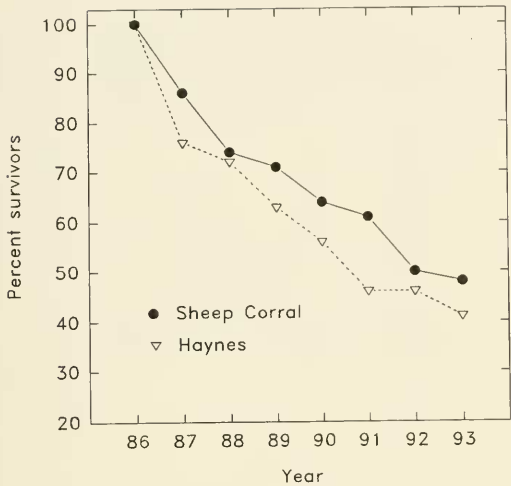


Fig. 2. Depletion curves for the 1986 sample populations of *Astragalus scaphoides* at the two study sites.

51% and 44% at Haynes Creek and Sheep Corral Gulch, respectively (Fig. 3).

Elasticity Analysis

Elasticity gives the proportional importance of demographic transitions to population growth. Elasticity matrices for five years of transitions for the two study sites are given in Table 2. Elasticities were summed into four life-history transition categories: (1) recruitment and survival and growth of (2) dormant, (3) nonreproductive, and (4) reproductive plants (Fig. 4). Growth and survival of nonreproductives was consistently important at both sites, with mean elasticities of 42% and 36% at Haynes Creek and Sheep Corral Gulch, respectively. Survival of dormant plants was important in two years at Sheep Corral Gulch and one year at Haynes Creek, with mean elasticities of 19% and 29%. Survival of reproductives had mean elasticities of 23% and 20% for the two sites, and mean elasticities for recruitment were 16% and 17%.

DISCUSSION

Loss of *Astragalus scaphoides* fecundity due to inflorescence and predispersal seed predation was high at both sites, ranging from ca 20% to >90%. Further losses in reproductive output due to ants or rodents may have occurred following dispersal. Recruitment was the least important stage transition in the life history of *A. scaphoides* during my study,

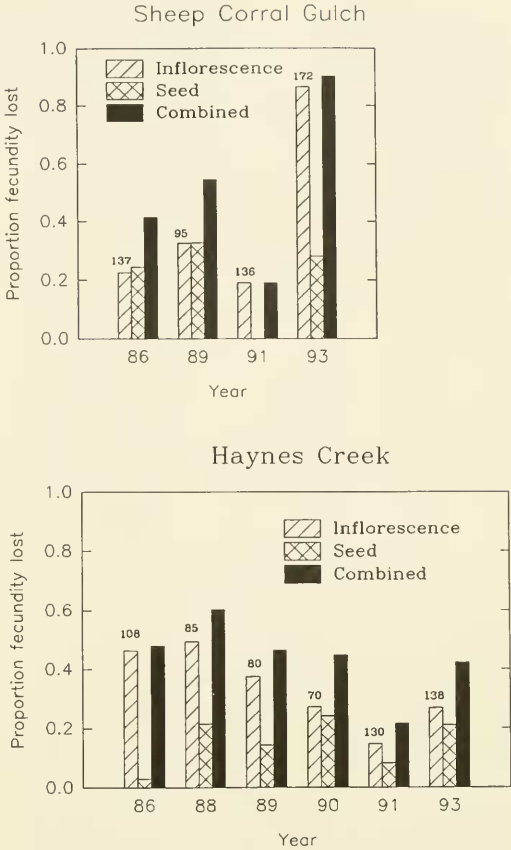


Fig. 3. Proportion of *Astragalus scaphoides* reproductive output lost to inflorescence predation, predispersal seed predation, and the combination of the two in those years when significant flowering occurred at two study sites. Numbers of inflorescences in samples are given above bars.

accounting for an average of less than 17% of population growth at both sites. High levels of inflorescence and seed herbivory are undoubtedly one of the main reasons for the low contribution of recruitment to λ in this species. Nonetheless, both sample populations became larger during the study. Furthermore, population growth rate was ≥ 1.0 in four of five years at both sites and never < 0.8 . Growth and survival of dormant and nonreproductive plants contributed $> 60\%$ to population growth at both sites. These results suggest that populations of *A. scaphoides* can persist and even grow larger in spite of heavy losses in reproductive output and low recruitment.

Large reductions in fecundity due to herbivores have been documented for *Astragalus* species (Green and Palmblad 1975) as well as

TABLE 2. Elasticities for *Astragalus scaphoides* stage transition matrices at two sites for 1987–1992. The left three columns (D, S, L) represent nonreproductive growth and survival. The reproductive (R) column represents growth and survival of reproductives. The recruitment column (Rc) represents recruitment from seed.

----- Sheep Corral Gulch -----											
1987-88						1990-91					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.048	.022	.015	0	0	D	.001	.005	0	0	0
S	.004	.032	.009	0	.024	S	.001	.018	.002	0	.185
L	.032	.015	.055	0	.077	L	.002	.082	.023	.014	.118
R	0	0	.101	.568	0	R	.003	.099	.215	.204	.029
1988-89						1991-92					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.001	.003	.001	0	0	D	.686	.126	0	0	0
S	.001	.017	.002	0	.139	S	.126	.061	0	0	0
L	.002	.081	.049	0	.143	L	0	0	0	0	0
R	.003	.057	.222	.224	.056	R	0	0	0	0	0
1989-90											
	D	S	L	R	Rc						
D	.413	.074	.015	.001	0						
S	.048	.292	.037	.002	.011						
L	.042	.007	.030	.005	.001						
R	0	.017	.002	.004	0						
----- Haynes Creek -----											
1987-88						1990-91					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.002	.003	.002	0	0	D	.001	.005	0	0	0
S	.001	.045	.002	0	.141	S	.001	.058	.004	0	.160
L	0	.082	.058	0	.153	L	.004	.080	.038	.046	.068
R	.003	.059	.231	.164	.055	R	.001	.079	.193	.264	0
1988-89						1991-92					
	D	S	L	R	Rc		D	S	L	R	Rc
D	.055	.048	.006	0	0	D	.617	.020	.041	.006	0
S	.007	.086	.020	.005	.113	S	0	.042	.030	.003	.005
L	.015	.064	.044	.028	.028	L	.068	.018	.082	.021	.001
R	.031	.034	.109	.287	.021	R	0	0	.036	.011	0
1989-90											
	D	S	L	R	Rc						
D	.081	.028	.013	0	0						
S	.023	.061	.024	.007	.039						
L	0	.065	.170	.093	.014						
R	.018	0	.134	.230	0						

many other plants (Janzen 1971, Hendrix 1988, Louda 1989). Louda (1982, 1983) has shown that seed predation can lead to lowered recruitment; however, reductions in seed output will not necessarily lead to reduced recruitment if germination safe sites are limiting (Harper 1977). Analysis of the matrix projection models suggests that recruitment is not limiting population growth of *A. scaphoides*. Recruitment from seed is likely to be important to population growth for short-lived species and is essential for semelparous ones. Furthermore, successful reproductive episodes are rare for some perennial species in rigorous

environments (Jordan and Nobel 1979). Significant reductions in a single reproductive bout could greatly increase chances of population extirpation for these sorts of species. On the other hand, many populations of long-lived plants will have more stable populations whose persistence is more dependent on the growth and survival of established plants (Silvertown et al. 1993). Survivorship curves indicate that *Astragalus scaphoides* is a long-lived species, and elasticity analysis suggests that recruitment is indeed less important to population persistence than growth and survival of nonreproductive plants.

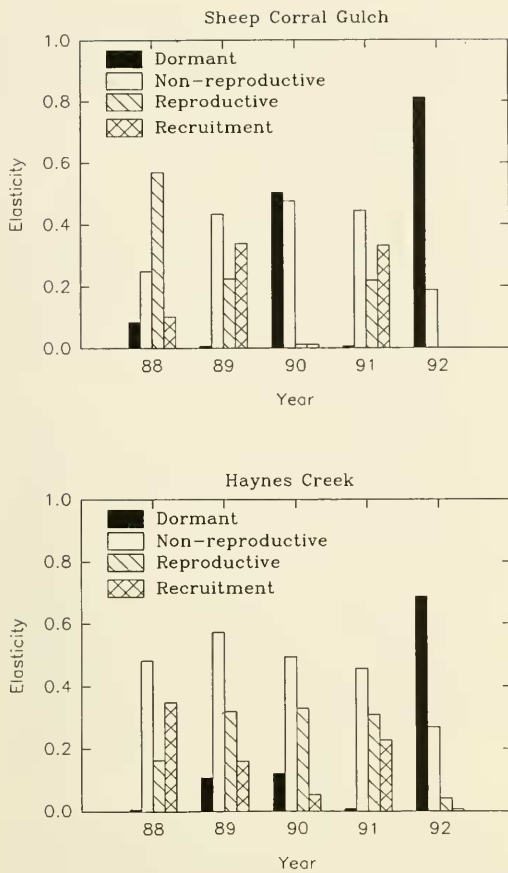


Fig. 4. Elasticities summed into four life-history transition categories (recruitment and survival and growth of dormant, nonreproductive, and reproductive plants) for *Astragalus scaphoides* at two study sites, 1987–1992.

Inflorescence predation of *Astragalus scaphoides* was greatest in years when livestock were present. In 1993 inflorescence predation was greater than 85%, and *A. scaphoides* was grazed in preference to the highly palatable grass, *Agropyron spicatum* (P. Lesica personal observation). These observations suggest that livestock could nearly eliminate reproductive output under high stocking rates and repeated heavy spring grazing if carried on over a long enough period of time. However, results of my study suggest that *A. scaphoides* populations can persist if predation is moderate, at least in some years. Rotation grazing systems in which spring grazing occurs only one in three years appear to be compatible with the long-term persistence of *A. scaphoides* populations.

These results have implications for other long-lived perennials exposed to livestock pre-

dation. Upper portions of plants are most accessible to livestock, and newer growth is generally selected by livestock (Arnold and Dudzinski 1978, Valentine 1990). Furthermore, sugars, such as found in flower nectar, also increase palatability (Arnold and Dudzinski 1978, Valentine 1990). Thus, livestock often remove only the upper portions of broad-leaved plants. Predation that mainly affects fecundity is likely to endanger populations only when grazing removes most inflorescences consistently for many years because population growth is not likely to be limited by recruitment. On the other hand, grazing that lowers growth and survival (e.g., high-density stocking during periods of growth) will have a much more detrimental effect on population viability.

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